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An Early Cambrian filter feeding anomalocarid

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Large, actively swimming filter feeders evolved several times in Earth's history, arising independently from groups as diverse as sharks, rays, teleost fishes¹, and in mysticete whales². Animals occupying this niche have not, however, been identified from the Early Palaeozoic. Anomalocarids, a group of stem arthropods that were the largest nektonic animals of the Cambrian and Ordovician, are generally thought to have been apex predators³⁻⁵. Here we describe new material of *Tamisiocaris borealis*⁶, an anomalocarid from the Early Cambrian Sirius Passet Fauna of North Greenland, and show that its frontal appendage is specialized for filter feeding. The appendage bears long, slender and equally spaced ventral spines furnished with dense rows of long and fine auxiliary spines. This suggests that it was a microphagous filter feeder, using its appendages for sweep-net capture of food items down to 0.5 mm, within the size range of mesozooplankton such as copepods. *Tamisiocaris* demonstrates that large, nektonic filter feeders first evolved during the Cambrian Explosion, as part of the adaptive radiation of anomalocarids. The presence of filter-feeders in the Early Cambrian, together with evidence for a diverse pelagic community containing phytoplankton^{7,8} and mesozooplankton^{7,9,10}, indicates the existence of a complex pelagic ecosystem supported by high primary productivity and nutrient flux^{11,12}. Cambrian pelagic ecosystems appear to have been more modern than previously believed, suggesting that the Cambrian explosion drove not only the origin of modern animal phyla but also modern marine food webs.

Anomalocarids are stem arthropods well known from the Cambrian and Ordovician¹³⁻¹⁶, and were the largest animals of their time. They are interpreted as nektonic apex predators, using their lateral flaps to swim in pursuit of prey, then seizing it with their raptorial frontal appendages^{3,16-18}. Recent discoveries have revealed a range of appendage morphologies^{14,17}, suggesting diverse feeding strategies, but the anomalocarids are not known to have exploited

1 plankton for food, which is a common nektonic strategy in modern oceans. In
2 fact, the first definitive evidence for large nektonic filter-feeders is from the
3 Mesozoic, when it evolved in the giant pachycormid fishes^{1,19} from the Jurassic
4 and Cretaceous, although there is some evidence to suggest that placoderm fish
5 may have exploited this niche in the Late Devonian¹⁹. Large nektonic filter
6 feeders are, however, unknown from the Early Palaeozoic.

7 *Tamisiocaris borealis*, from the Early Cambrian Sirius Passet fauna of
8 North Greenland, has previously been described as a possible anomalocarid on
9 the basis of a disarticulated frontal appendage⁶. New fossils not only substantiate
10 the anomalocarid affinities of *Tamisiocaris*, but also show that it was adapted to
11 prey microphagously on mesozooplankton.

12 *Tamisiocaris borealis* is known from six isolated frontal appendages and
13 two appendages associated with a head shield. Frontal appendages (Fig. 1)
14 measure ≥ 120 mm in length, comparable in size to the later *Anomalocaris*
15 *canadensis*¹³. As in other anomalocarids, the appendage consists of discrete,
16 sclerotized articles. All specimens are preserved with the ventral spines parallel
17 to the bedding plane, and the articles show no evidence of distortion due to
18 compaction. It is therefore assumed that the articles were transversely
19 compressed, with an oval cross section in life. The appendage consists of at least
20 18 articles, versus 14 in, for example, *A. canadensis*. Articles are separated by
21 triangular arthrodial membranes (Extended Fig. 2b,c). These extend almost to
22 the dorsal margin of the appendage; ventrally, the membrane is 33-50% the
23 length of the articles, suggesting a well-developed flexural ability.

24 The appendage curves downward distally, with the strongest curvature
25 around the second and third article. The first article is straight, and longer than

1 the next three combined. It bears a single pair of ventral spines near its distal
2 margin, which are stout and angled backwards (Fig. 1a) as in *Anomalocaris*
3 *briggsi*⁵. The next 17 articles each bear pairs of long and delicate ventral spines
4 inserted at the mid-length of the article. These are evenly spaced along the
5 appendage about 5-6 mm apart. The spines diverge ventrally such that each pair
6 forms an inverted V-shape. Unlike *A. canadensis*, in which longer and shorter
7 spines alternate and taper distally, the ventral spines are all of similar length,
8 measuring 26-27.5 mm along the full length of the appendage (fig. 1a,b, Extended
9 data Fig. 1-3). A similar condition is seen in *A. briggsi*. The ventral spines curve
10 posteriorly, again as in *A. briggsi*, but unlike any other anomalocarids. Individual
11 spines appear flattened, with a median rod and thinner lamellar margins
12 (Extended data Fig. 1c). In addition, ventral spines are frequently kinked, and
13 sometimes broken, suggesting that they were weakly sclerotized and flexible.

14 As in many other anomalocarids^{5,14}, the anterior and posterior margins of
15 the ventral spines bear auxiliary spines (Fig. 1c, Extended data Fig. 1c, 2d, 3), but
16 they are unusually long in *Tamisiocaris* —measuring 4.2-5.0 mm in length— and
17 extremely slender. Auxiliary spines form a comblike array, being spaced 0.3-.85
18 mm apart, with a median spacing of 0.49 mm. The length and spacing are such
19 that adjacent spine combs would overlap or interdigitate.

20 One specimen consists of two associated appendages in subparallel
21 orientation (Extended data Fig. 4). Proximally, they join a large, elliptical head
22 shield. The headshield is larger than in *Anomalocaris canadensis*, but is not
23 enlarged to the same degree as seen in *Peytoia nathorsti* and *Hurdia victoria*.

24

25 The affinities of *Tamisiocaris* were examined in a cladistics analysis to

1 explore its position within the anomalocarids. The analysis recovers a clade
2 consisting of *Tamisiocaris borealis* and *Anomalocaris briggsi* (Fig. 4). This clade,
3 the Cetiocarididae (n. nom), is diagnosed by long, slender, and recurved ventral
4 spines, and the presence of numerous auxiliary spines. *Tamisiocaris* is more
5 specialized, however, in having flexible ventral spines and densely packed
6 auxiliary spines. The cetiocaridids are a sister to the Hurdiidae, a clade
7 containing *Hurdia victoria*, *Peytoia nathorsti*, and related species. Outside these
8 taxa lies a clade of presumably plesiomorphic forms including *Anomalocaris*
9 *canadensis*, *A. saron*, *Amplectobelua* spp., and relatives.

10 The hypothesis that *Tamisiocaris borealis* engaged in filter feeding can be
11 tested by comparisons with extant analogues (Extended data Figure 5).
12 Suspension feeding crustaceans, such as cirripedes (barnacles), atyid shrimp,
13 copepods, cladocerans, mysids and euphausiaceans (krill) share a suite of
14 adaptations for sieving particles out of the water column which are very similar
15 to the appendages in the cetiocarididae (Extended data figure 5). These include
16 appendages with (i) very elongate, flexible setae and/or setules and (ii) regular
17 spacing. These features create a net with a regular mesh size that efficiently traps
18 all particles above a threshold set by the appendage spacing. The feeding limbs
19 sieve particles out of the water, concentrate them by contraction, and carry them
20 to the mouth²⁰. The filter feeding apparatuses of vertebrates have a similar
21 morphology. Filter-feeding teleosts and some sharks use a mesh formed by long,
22 slender, and closely spaced gill rakers. The feeding apparatus of mysticete
23 whales consists of arrays of baleen plates that wear into elongate fringes²¹.

24 The mesh size of the capture apparatus is closely related to prey size:
25 Right whales specialise on small copepods (fringe diameter 0.2 mm) while blue

1 whales (fringe diameter 1 mm), feed on larger krill²². A survey of diverse
2 suspension feeders, from cladocerans to blue whales, shows a linear relationship
3 between mesh size and minimum prey size (Fig. 4). While larger prey can be
4 captured, the bulk of the prey is close to the mesh size of the filter apparatus.

5 Based on the morphologies seen in modern animals, a filter-feeding
6 anomalocarid would be predicted to have evolved a setal mesh, with large
7 appendages bearing long, flexible setae to increase capture area, with regular
8 setal spacing. This is indeed the morphology observed in *Tamisiocaris*.
9 Furthermore, one can use the mesh dimensions to predict the size of the prey
10 caught by *Tamisiocaris*. Spacing of the auxiliary spines in *T. borealis* suggests that
11 it could filter food items from the water column down to 0.5 mm, while linear
12 regression from extant filter feeders (Fig. 4) predicts a slightly larger minimum
13 particle size of 0.71 mm. Known mesozooplankton, from small carbonaceous
14 fossil assemblages from the Cambrian Series 2^{9,10}, include isolated feeding
15 appendages from crustaceans, including putative copepods. Based on
16 comparisons with mandibles of modern counterparts¹⁰ the largest known
17 specimens reached diameters of 1.5 to 2.7 mm. The filter appendage of *T.*
18 *borealis* predicts mesozooplankton of much smaller diameters yet to be
19 described. Feeding was probably accomplished by alternate sweeping of the
20 appendages, with entrapped prey being sucked up by the oral cone
21 (Supplementary information animation 1 and 2).

22 In the context of the phylogenetic analysis presented here, *Tamisiocaris*
23 appears to have been part of an adaptive radiation of anomalocarids, with
24 different clades evolving distinct frontal appendage morphologies and feeding
25 strategies. Primitive forms such as *Anomalocaris canadensis* had raptorial

1 appendages with stout, trident-like spines, well-suited to impaling large, free-
2 swimming or epifaunal prey³ (Extended data Fig. 6a). *Amplectobelua* had pincer-
3 like appendages²³ (Extended data Fig. 6b) that would have been effective in
4 seizing and tearing apart relatively large, slow-moving animals. In hurdiids, the
5 appendages bear opposing pairs of spines, which may have functioned as jaws or
6 in sediment sifting¹⁴ (Extended data Fig. 6c). Finally, cetiocaridid frontal
7 appendages are specialized as sweep nets (Extended data Fig. 6d,e). This
8 extraordinary range of appendage morphologies shows that, far from being a
9 failed experiment, anomalocarids staged a major adaptive radiation during the
10 Cambrian Explosion, evolving to fill a range of niches as nektonic predators,
11 much like the later radiations of vertebrates¹⁹ and cephalopods²⁴, by also
12 becoming secondary filter feeders.

13 The existence of filter feeding in anomalocarids also has implications for
14 the structure of Early Cambrian pelagic food webs (Extended data Fig. 7). It had
15 been assumed that a diverse planktonic fauna and suspension feeding animals
16 did not evolve until the Late Cambrian²⁵ and thus the complexity of the pelagic
17 food web evolved in a delayed, piecemeal fashion. However, the discovery of
18 large filter feeders in the Early Cambrian suggests a well-developed pelagic biota
19 supported by high primary productivity and abundant mesozooplankton,
20 because large animals can only exploit small prey when they exist at high
21 densities. Whales, whale sharks and basking sharks exploit highly productive
22 areas such as upwelling zones and seasonal plankton blooms at high latitudes²⁶.
23 This general observation holds for all microphagous suspension feeders ranging
24 from cladocerans, to anchovies, to red salmon, to blue whales: a high density of
25 food particles is required to sustain an actively swimming filter feeder.

1 *Tamisiocaris* therefore indicates high productivity at the time of
2 deposition at Sirius Passet. Other evidence suggests that high productivity may
3 have been a global phenomenon in the Cambrian provided by vast deposits of
4 phosphorites and increased terrestrial nutrient flux^{11,12,27}. Furthermore, the
5 Cambrian also witnessed a radiation of spiny acritarchs, which presumably
6 evolved into microscopic phytoplankton replacing the larger Neoproterozoic
7 benthic forms^{7,8}. Complex minute crustacean feeding appendages also occur in
8 lower and middle-upper Cambrian rocks^{9,10}, demonstrating the presence of
9 diverse mesozooplankton preying on phytoplankton. Abundant vetulicolians in
10 Sirius Passet²⁸ (100s of specimens collected on recent expeditions) may also
11 have suspension fed upon phytoplankton (Extended data fig. 6). One tier up,
12 *Tamisiocaris* would have preyed upon the mesozooplankton as would the
13 common bivalved nektonic arthropod *Isoxys volucris*²⁹. Other pelagic predators
14 known from Lagerstätten elsewhere would likewise have fed on
15 mesozooplankton, including ctenophores, cnidarians, chaetognaths and pelagic
16 arthropods (Extended data Fig. 6). The Cambrian pelagic food web was therefore
17 highly complex, containing multiple trophic levels, including pelagic predators
18 and multiple tiers of filter-feeders. This underscores the remarkable speed with
19 which a modern food chain was assembled during the Cambrian Explosion.

20 Finally, the discovery of a filter feeding anomalocarid has implications for
21 debates concerning the predictability of evolution, or lack thereof. One view
22 holds that evolution is ultimately unpredictable³⁰. The striking convergence
23 between *Tamisiocaris* and extant filter feeders, however, suggests that while
24 ecological niches are occupied by different groups at different times, the number
25 of viable niches and viable strategies for exploiting them are limited.

1 Furthermore, the derivation of the filter-feeding *Tamisiocaris* from a large apex
2 predator parallels the evolution of filter feeding pachycormid fish^{1,19}, sharks and
3 whales². In each case, filter feeders evolved from nektonic macropredators. This
4 suggests that evolution is constrained not only in terms of outcomes, but in
5 terms of trajectories. The result is that independent evolutionary experiments by
6 animals as different as anomalocarids, fish and whales have converged on
7 broadly similar outcomes.

8

9 METHODS SUMMARY

10 Specimens were collected in the field and photographed in the lab, coated or
11 uncoated submerged in water. A digital reconstruction of the *Tamisiocaris*
12 feeding appendage were made in order to infer the range of motions. The filter
13 mesh diameter and prey width were collated from extant filter feeders to depict
14 the linear relationship between these (see Methods). A cladistics analysis
15 containing XX taxa and XX characters were collated and analysed in Paup and
16 TNT, see Supplementary information.

17

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- 23
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25

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32

33

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37

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40 Readers are welcome to comment on the online version of the paper.
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43

44 **Figure 1 | *Tamisiocaris borealis* Daley and Peel, 2010 frontal appendages**

45 **from Sirius Passet, Lower Cambrian, North Greenland. a, Isolated and**

1 relatively complete appendage, MGUH XXXXX. **b.** Isolated appendage, preserving
2 auxiliary spines in great detail, MGUH XXXXX. **c.** detail of spine in **b.** All specimens
3 photographed submerged in water with high angle illumination.

4
5 **Figure 2 | A digital reconstruction of *Tamisiocaris*.** **a.** Single appendage
6 indicating the articulating membranes (Am), articles (Art), spines (Sp) and
7 auxiliary spines (As). **b.** Possible sequence of movement of the frontal
8 appendage of *Tamisiocaris*. See also extended data movies 1 and 2.

9
10 **Figure 3 | Diagram depicting the relationship between filter mesh size and**
11 **the food items consumed by suspension feeders.** *Tamisiocaris* is indicated by
12 the dotted line based on a mesh width of 0.51 mm. The diagram is collated from a
13 range of modern filter feeders, see Methods section.

14
15 **Figure 4 | Phylogeny of anomalocarids.** Cladistics analysis based on XX
16 characters and including XX taxa analyzed in Paup and TNT. *Tamisiocaris* form a
17 clade with *Anomalocaris briggsi*, which are here named Cetiocaridae.

18
19 **Extended data figure 1 | *Tamisiocaris borealis* MGUH XXXXX, frontal**
20 **appendage.** **a.** Part photographed in low angle lighting coated with MgO with
21 indications of spines (s1-s15); spines, broken at the base (bs). **b.** Camera lucida
22 drawing **c.** detail of spine preserving auxiliary spines in relief.

23
24
25 **Extended data figure 2 | *Tamisiocaris borealis* MGUH XXXXX, frontal**

1 **appendage. a.** Part, photographed submerged in water and with high angle
2 illumination. **b.** Counterpart, displaying articulating membranes across the
3 appendage indicated by their relatively lower reflectivity. **c.** Detail of **b**, and the
4 articulating membranes along the mid section of the appendage. **d.** Detail of
5 broken spine in **b**, displaying auxiliary spines in.

6
7 **Extended data figure 3 | Tamisiocaris borealis MGUH XXXXX frontal**

8 **appendage with well preserved auxiliary spines. a.** Part. **b.** detail of auxiliary
9 spines in **a**. **c.** schematic drawing of MGUH XXXX, from a combination of part and
10 counterpart. **d.** Counterpart. **e.** Detail of **d**.

11
12 **Extended data figure 4 | MGUH XXXXXX frontal appendages and head shield**

13 **assemblage. a.** Part. **b.** Camera lucida drawing of the part indicating the head
14 shield (Hs), left frontal appendage (Lfa) and right frontal appendage (Rfa)

15
16 **Extended data figure 5 | Modern crustacean filter feeders. a.** the Northern

17 krill, *Meganyctiphanes norvegica* (Image credit: Wikipedia/Øystein Paulsen).
18 Insert: reconstruction of the thoracic region of the krill, *Euphausia superba*, from
19 Barkley (1940). **b.** Proximal elements of the thoracopods in *E. superba* (Image
20 credit, Uwe Kils). **c.** Distal elements of the thoracopods in *E. superba* (Image
21 credit, Uwe Kils). **d.** The filter basket in an undetermined mysid (Image credit
22 Wikipedia/Uwe Kils). **e.** Thoracopod from the cirripede *Darwiniella angularis*
23 Chen, Lin and Chan 2012, with permission from the authors.

24
25 **Extended data figure 5 | Schematic drawings of different anomalocarid**

1 **frontal appendages to scale, indicating their likely function. a. *Anomalocaris***
2 ***canadensis*, b. *Amplectobelua symbrachiata*, c. *Hurdia victoria*, d. *Anomalocaris***
3 ***briggsi*, e. *Tamisiocaris borealis*.**

4
5 **Extended data figure 6 | A schematic overview of known components the**
6 **Early Cambrian pelagic food web.** At the base of the food chain was
7 phytoplankton in the form of acritarchs and most likely other forms with no
8 apparent fossil record. Diverse mesozooplankton were present as copepod and
9 branchiopod-like crustaceans feeding on phytoplankton, along with the
10 vetulicolians, which exhibit a morphology suggesting filter feeding similar to
11 basal chordates. Larger pelagic predators such as chaetognaths, larger
12 arthropods and potentially also ctenophores preyed upon the mesozooplankton.
13 *Tamisiocaris* would similarly have fed on the mesozooplankton. The presence of
14 a large nektonic suspension feeder suggests a high abundance of primary
15 producers and mesozooplankton. Other anomalocarids, such as *Anomalocaris*
16 and *Amplectobelua* were present as some of the macrophagous apex predators at
17 this time.

18